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Onshore-offshore trend in the evolution of calliotropid gastropods expressed in shell morphology

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Two new species of calliotropid gastropods, *Calliotropis* (*Riselloidea*) *faustiankensis* sp. nov. and *Calliotropis* (*Riselloidea*) *lukovensis* sp. nov., are described from the Middle Jurassic (Middle Bathonian−Upper Callovian) of Poland. Additionally, new excellently preserved shells of *Calliotropis* (*Riselloidea*) *biarmata* (Münster) allow redefinition of this species. The new morphological information obtained from these three fossil species of *Calliotropis* in combination with the dataset assembled from 20 extinct and 24 living calliotropids is here summarized in quantitative multivariate and principal component analyses suggesting an onshore-offshore trend in calliotropid gastropod evolution from the Triassic to Recent times. This trend, which is expressed in the morphology of shells, shows that the Mesozoic species are mostly shallow water, while Cenozoic and Recent taxa are mostly deep water. The distinction supports earlier suggestions that the genus *Calliotropis* can be subdivided into two temporal subgenera belonging to the family Eucyclidae Koken.

http://zoobank.org/urn:lsid:zoobank.org:pub:C8362FB8-966A-4322-95D5-7151CED20476

Introduction

Species of *Calliotropis* Seguenza, 1902 display a strong morphological conservatism, with Cenozoic and modern forms being strikingly similar to the Jurassic species. The systematic position of the genus was discussed by Ferrari *et al*. (2014) who accommodated it in the family Eucyclidae. According to the molecular data of Kano (2008) and Kano *et al*. (2009), the extant species of *Calliotropis* belong to the monophyletic family Calliotropidae within the superfamily Seguenzoidea. Kano (2008) also suggested that Seguenzioidea comprises the families Seguenziidae, Chilodontidae, Cataegidae and Calliotropidae – all having modern representatives – while the Mesozoic Eucyclidae may represent an ancestral branch of Seguenzioidea.

The distinction between fossil and modern calliotropids dates from the monograph of Hickman & McLean (1990) who treated Eucyclidae as an extinct family with maximum diversity in shallow seas of the Jurassic but declining towards the Cretaceous. They introduced the new family name Calliotropidae for the Cenozoic forms that diversified due to the radiation of the group into deep water, uniting taxa previously classified under a variety of trochoidean family-group names (Hickman 2016). Kaim (2004) suggested that both fossil (i.e. *Riselloidea*) and modern (i.e. *Calliotropis*) species should be united into the genus *Calliotropis* on morphological grounds. Since that time, the classification of calliotropids has been a matter of debate. Some researchers have followed the recommendation of Kaim (2004) (e.g. Gründel & Koppka 2007) while some others (e.g. Bandel 2010) have preferred to keep fossil and living species in separate families. More recently, Ferrari *et al*. (2014) proposed the classification of both groups into two temporal subgenera: *Riselloidea* for fossil species and *Calliotropis* for modern species. According to Ferrari *et al*. (2014) the major difference between *Calliotropis* and *Riselloidea* is the absence of an umbilicus and the presence of a smaller and more depressed protoconch in the latter. The shells of modern calliotropids are generally umbilicate and possess large bulbous protoconch. The complexity of the problem highlighted is exemplified by the presence of an umbilicus in some Jurassic species, e.g. *C.* (*R.*) *multistriata* and *Calliotropis* (*R.*) *erratica*. In spite of this, it is now clear that calliotropids represent an ancient radiation of seguenzioids with relatively stable shell morphology.

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The preliminary arbitrary division of *Calliotropis*-like species into two subgenera by Ferrari *et al.* (2014) was made without detailed analysis of all taxa in question. Here we address this problem in more detail based on a survey of published information and new excellently preserved Middle Jurassic calliotropids from Poland. We have assembled all available morphological information from the shells of calliotropids in a dataset, along with ecological and palaeoecological information for particular living and fossil taxa and have performed quantitative multivariate and principal component analyses to search for patterns in the evolution of this group. Finally, we elucidate the evolutionary and biological relationships between fossil and modern forms, attempting to clarify the misunderstandings which have arisen around the taxonomic status of these gastropods.

Material and methods

The new material investigated here comes from collections housed at the Institute of Paleobiology, Polish Academy of Sciences, Warszawa, Poland (**ZPAL**) and collected mostly by AK in field seasons from 1995−2012. Some additional material was collected by AK and MF in 2015. The material comes from two localities in the Częstochowa region (Faustianka and Kawodrza-Sowa) and one in the Podlasie region (Łuków), both representing Middle Jurassic clay facies deposited in an outer shelf environment (Kaim 2004, 2008; Gedl & Kaim 2012). The small specimens were washed from the sediment using sieves while larger ones were collected individually in the field. After cleaning specimens were mounted on stubs and coated with platinum for SEM examination.

Morphological terminology follows Cox (1960), Vilvens (2007), Kaim (2004), Ferrari *et al.* (2014) and Hickman (2016).

Statistical methods

We performed two quantitative morphological analyses: cluster analysis (with Ward's algorithm) and principal component analysis (PCA) using the statistical software PAST (Hammer *et al.* 2001). The data considered in the analyses integrates 47 species of *Calliotropis* species represented in the fossil record and at the present-day worldwide. Shell diagnostic characters, such as spire angle, basal angle, umbilical width, apertural inclination, morphology of the aperture and the outer lip, columellar denticle, size (H), height/width (H/W) ratio (as a measurement of the spire height), protoconch width, and protoconch and teleoconch ornament, were examined in the selected *Calliotropis* species, taking into consideration their significance in gastropod taxonomy and biological function (Fig. 1; Supplemental Tables 1, 2). Protoconch
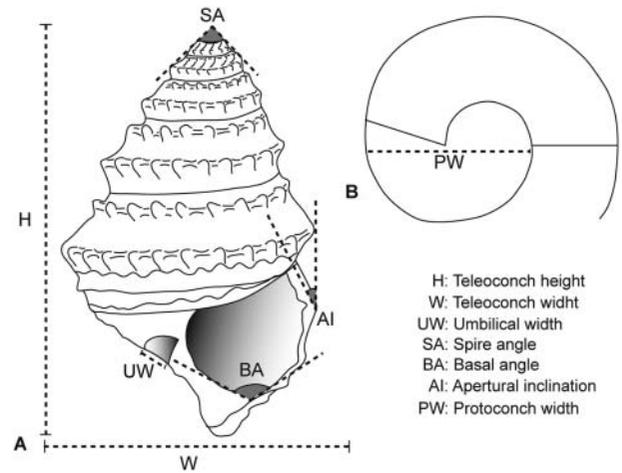
Figure 1. Measurements used to evaluate patterns of morphological evolution in *Calliotropis* species. **A,** adult teleoconch; **B,** protoconch.

ornament was included in the analysis although this character is missing in the majority of the fossil gastropods. In any case, protoconchs in vetigastropods are relatively conservative and have limited value in species-level phylogenetics (cf. for higher rank systematics, e.g. Geiger *et al.* 2008).

The fossil species of *Calliotropis* included in the analyses occur in Mesozoic and Cenozoic marine deposits worldwide (Asia, Europe, South America, Australia, Antarctica and Philippines) and represent a wide timespan (Late Triassic to Plio-Pleistocene). The greatest abundance of this group is recorded along the Jurassic Western European epicontinental seashore of Tethys, mostly known in shallow water and reef-associated palaeoenvironments (Supplemental Table 1). Within the extinct *Calliotropis*, almost all of the species recovered from the fossil record were examined.

Regarding living *Calliotropis*, which are diverse and numerous, species were selected to represent taxonomic diversity, and the concepts of Vilvens (2007) and Hickman (2016) were followed. Most of the living species of *Calliotropis* occur in the Indo-Pacific, and among this fauna shell size was considered as an important feature, with large sized (H > 15 mm), medium-sized (H = 6–15 mm) and small-sized (H < 6 mm) shells included. Spire ratio (H/W) was also considered to be an important character in the selection of species, with measurements being made of high- spired (H/W $<$ = 7), moderately high- spired ($0.7 < H/W < 1$) and depressed- spired (H/W $<$ = 7) shells. The presence of an umbilicus, columellar denticle, descending aperture and reflected outer lip were also used when selecting living species, and species occurring at a wide span of bathymetric and geographical ranges were also included (see Supplemental Tables 1, 2). The dataset includes continuous and categorical

variables. Continuous variables were discretized into categorical variables for the multivariate analyses. The character measurements of the fossil and living selected species were based on photographs, digital images of museum specimens, published figures and original samples.

Fossil localities

The Polish Jurassic material of *Calliotropis* came from Kawodrza-Sowa, Faustianka and Łuków in the Często-chowa and Podlasie regions.

Kawodrza-Sowa. This locality is a brick-pit located on the western rim of Częstochowa. The section exposed about 6 m of grey silty clay at the Bajocian–Bathonian boundary (Matyja & Wierzbowski 2000). The *Calliotro-pis* material described here comes from the upper part of the section, representing the uppermost *Parkinsonia*

bomfordi Subzone of the Late Bajocian, just below the 'D' ironstone layer of Matyja & Wierzbowski 2000 (see Kaim 2004; Fig. 2).

Faustianka. This is an abandoned brick-pit located in the eastern part of the village of Faustianka. At the time of collection (2003) the section exposed about 8 m of black to grey clay with layers of ironstone nodules. The samples yielding *Calliotropis* occur in the *Procerites progracilis* Zone of Middle Bathonian age (Matyja & Wierzbowski 2000) and were taken from the upper part of the section (see Kaim 2004; Fig. 2).

Łuków. This is an abandoned brick-pit at Łapiguz, a sub-urb in the southern part of Łuków town. The outcrop exposed the Late Callovian black clay with limestone con-cretions containing a rich ammonite fauna. The concre-tions are from the *Quenstedtoceras henrici* Subzone of
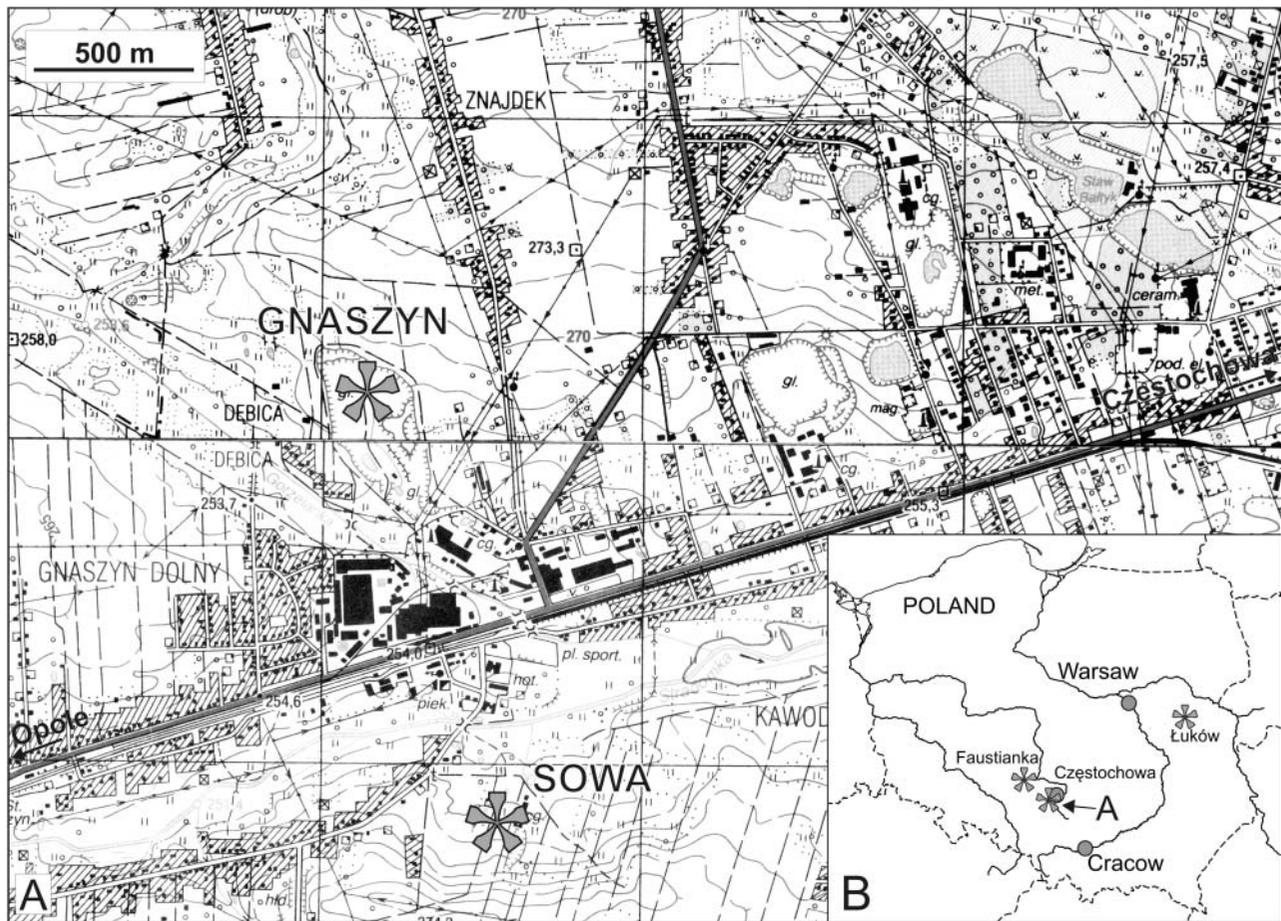
Figure 2. Locality map of the western outskirts of Częstochowa (**A**) and general map of Poland (**B**) indicating positions of localities discussed.

Late Callovian age. The rocks at Łuków are foreign to the area: autochthonous Late Callovian strata reached by deep boreholes in the Łuków area were deposited in carbonate facies, whereas the source of the Callovian clay is probably the bottom of the Baltic Sea north of Gdańsk (Kaim 2004, 2008; Fig. 2).

Systematic palaeontology

Class **Gastropoda** Cuvier, 1795
Subclass **Orthogastropod**a Ponder & Lindberg, 1997
Order **Vetigastropoda** Salvini-Plawen, 1980
Superfamily **Seguenzoidea** Verrill, 1884
Family **Eucyclidae** Koken, 1897
Genus *Calliotropis* Seguenza, 1902

Type species. *Trochus ottoi* Philippi, 1844 by monotypy; Pleistocene of Sicily, Italy. This species has been recognized as a still living member of *Calliotropis* in the Mediterranean Sea and in the eastern and northern Atlantic Ocean (e.g. Kaim 2004; Bandel 2010).

Occurrence. Upper Triassic–Middle Jurassic of western Europe, India and South America; Upper Cretaceous of Spain; Paleocene of Australia; Eocene of Antarctica; cosmopolitan in the Holocene.

Remarks. Ferrari *et al*. (2014) pointed out that the most important shell characters useful for defining species of *Calliotropis* are shell profile, adult size, sculpture and umbilical development. Hickman (2016) argued that size and shape terms, measurements, ratios, angles, whorl counts, and counts of sculptural elements are useful for defining ranges of variation within species and have a descriptive rather than diagnostic value. She introduced some morphological terms for new deep sea *Calliotropis* species from the Indo-Pacific, including the recognition of a reflected outer lip, a descending aperture, complete or partially closed open umbilicus and a columellar denticle. All of the shell features mentioned above are here considered as diagnostic of *Calliotropis*. Moreover, new protoconch ornament characters found in the Jurassic species of *Calliotropis* described here strongly relate these forms to contemporary counterparts in the families Seguenziidae Verrill, 1884 (*Seguenzia* Jeffreys, 1876, *Calliobasis* Marshall, 1983, *Halystina* Marshall, 1991, *Adeuomphalus* Seguenza, 1876), Calliotropidae Hickman & McLean, 1990 and Chilodontidae Wenz, 1938 (*Calliomphalus* Cossmann, 1888, *Euchelus* Philippi, 1847, *Danilia* Brusina, 1865, *Ilerdus* Calzada, 1989). The Mesozoic representatives of *Calliotropis* are here assigned to the ancient family Eucyclidae Koken, 1897 and accommodated within the subgenus *Riselloidea*. According to Bouchet

et al. (2017), the family Calliotropidae Hickman & McLean, 1990 is a junior synonym of Eucyclidae.

Subgenus *Riselloidea* Cossmann, 1909

Type species. *Calliotropis* (*Riselloidea*) *subdisjuncta* (Cossmann, 1909), from the Early Jurassic of northern France.

Remarks. The genus *Riselloidea* was downgraded by Ferrari *et al*. (2014) to subgeneric status to include fossil representatives of *Calliotropis* without strong morphological reasons for this taxonomic assignment, apart from the considerable difference in geological age. The quantitative morphological analyses undertaken here (see below) group within *Calliotropis* (*Riselloidea*) shells that have a strong reticulate ornament pattern consisting of primary and secondary spiral cords forming nodes at the crossing points and conspicuous or spinose nodes at the periphery of the whorls. They lack a widely opened umbilicus or, eventually, have a very narrow umbilical area or pseudoumbilicus, and comprise high- to moderately high-spired and medium sized shells. They completely lack the descending aperture and the reflected outer lip, and are usually without the columellar denticle. The protoconch is of smaller size than those of living members – although the ornament displays no differences between modern and Mesozoic forms – and is characterized by the presence of numerous pits forming a net-like pattern.

Included species. *Calliotropis* (*Riselloidea*) *aliabadensis* Nützel & Senowbari-Daryan, 1999, *Calliotropis* (*R.*) *naybandensis* Nützel & Senowbari-Daryan, 1999, *Calliotropis* (*R.*) *iranicus* (Nützel *et al.,* 2003), *Calliotropis* (*R.*) *subdisjuncta* (Cossmann, 1909), *Calliotropis* (*R.*) *vaihingensis* (Brösamlen, 1909), *Calliotropis (R.) noszkyi* Szabó, 1995, *Calliotropis* (*R.*) *multistriata* (Böckh 1874), *Calliotropis* (*R.*) *erratica* Gründel & Koppka, 2007, *Calliotropis* (*R.*) cf. *keideli* (in Ferrari *et al.*, 2014), *Calliotropis* (*R.*) *keideli* Ferrari *et al.*, 2014, *Calliotropis* (*R.*) *lorioli* (Greppin, 1898), *Calliotropis* (*R.*) *biarmata* (Münster, 1844), *Calliotropis* (*R.*) *tagorei* Das *et al.*, 1999, *Calliotropis* (*R.*) *elongata* Das *et al.*, 1999, *Calliotropis* (*R.*) *pileiformis* Jaitly *et al.* (2000), *Calliotropis* (*R.*) *vierowiensis* Gründel, 2000, *Calliotropis* (*R.*) *seguris* Kiel & Bandel, 2001, *Calliotropis* (*R.*) *microglyptophorus* Darragh, 1997, *Calliotropis* (*R.*) *antarchais* Stilwell, 2005, *Calliotropis* (*R.*) *torallolensis* Kiel & Bandel, 2001, *Calliotropis* (*R.*) *arenosa* Helwerda *et al.*, 2014, *Calliotropis* (*R.*) *faustiankensis* sp. nov. and *Calliotropis* (*R.*) *lukovensis* sp. nov.

Calliotropis (*Riselloidea*) *biarmata* (Münster, 1844)
(Fig. 3A–J)

1844 *Trochus biarmatus* Münster: 55, pl. 170, fig. 2.

2

2003a *Biarmatoidela biarmata* (Münster, 1844); Gründel: 65, pl. 6, figs 5–8.

2004 *Calliotropis biarmata* (Münster, 1844); Kaim: 22, fig. 9B–E.

2012 *Riselloidea biarmata* (Münster, 1844); Gründel *et al.*: 20.

Emended diagnosis. Protoconch of 0.4 mm diameter, dome-shaped, symmetrically paucispiral, sculptured by numerous pits forming a net-like pattern, consisting of 1.5 whorls; conical teleoconch, cytoconoid on earliest whorls, coeloconoid on mature whorls; H/W ratio < 1.2 in juvenile; H/W ratio ≥ 1.2 in adults; axial ribs dominate on juvenile whorls; later in ontogeny whorls angulate at two keels; pointed and acute nodes at the spiral keels on mature whorls; a third secondary and weak spiral cord emerging from suture at third whorl; strongly prosocline growth lines visible on later whorls; base convex to flattened, sculptured by three nodular spirals; aperture quadrangular and pseudoumbilicated in juvenile shells and sub-circular in adult specimens; columellar lip thickened as a moon-shaped callus which covers the pseudoumbilical area.

Material. ZPAL Ga. 18/1−35, Kawodrza−Sowa (Fig. 2), Poland, Late Bajocian.

Occurrence. Middle and Late Jurassic of Europe.

Description. Dextral, small-sized, conical, cyrtoconoid on earliest whorls to slightly coeloconoid toward mature growth stages, and moderately high-spired shell. Protoconch convex, slightly depressed and dome-shaped, symmetrically paucispiral, consisting of 1.5 whorls with a width of 0.4 mm, and sculptured by small, irregular, somewhat microhexagonal granules that connect to form a net-like

pattern and are more clearly visible on the adapical and abaxial margin. Clear demarcation between protoconch and teleoconch. Teleoconch of adult specimens consists of 7 whorls, with a mean height of 7.6 mm and a mean width of 6.6 mm. The spire angle is 70° and the basal angle is 135°. The suture is impressed in a concave furrow. Juvenile shells show a height/width ratio of < 1.2; adult teleoconchs exhibit a height/width ratio of ≥ 1.2 (Fig. 4). These ontogenetic changes show that there is an increment in the translation rate as the shell grows, mature teleoconchs being larger in respect to their width than juvenile teleoconchs (Fig. 4). First teleoconch whorl strongly convex starting with ortho-cline to slightly prosocline axial ribs which run from suture to suture and number 20–23 per whorl; axial ornament is predominant at the earliest teleoconch whorls and spiral ornament is feeble; towards the third and fourth whorls axial ribs become stronger, prosocline and regularly spaced. Spiral ornament is clearly visible at the third whorl; it consists of two primary spiral ribs bordering the sutures and located in abapical and adapical position of the flanks; small and rounded nodes appear on the primary spiral cord at the third whorl. From fifth whorl towards the mature growth stages axial ribs become feeble and fade away on the last whorl. The two primary spiral ribs are stronger towards the mature stages and nodes are also stronger and pointed; a third weakly developed spiral cord emerges from the suture at the third whorl. The third spiral cord becomes stronger and peripheral with rounded nodes towards the last whorl. Nodes are acute and pointed on the spiral cords of mature whorls, and number 14–15 on the juvenile whorls increasing to 18–20 on adults. On the last whorl, the third nodular peripheral spiral cord is fully visible and emerges from the abapical suture. Nodes on the abapical and third peripheral spiral cords are regularly spaced and equally developed. Strongly
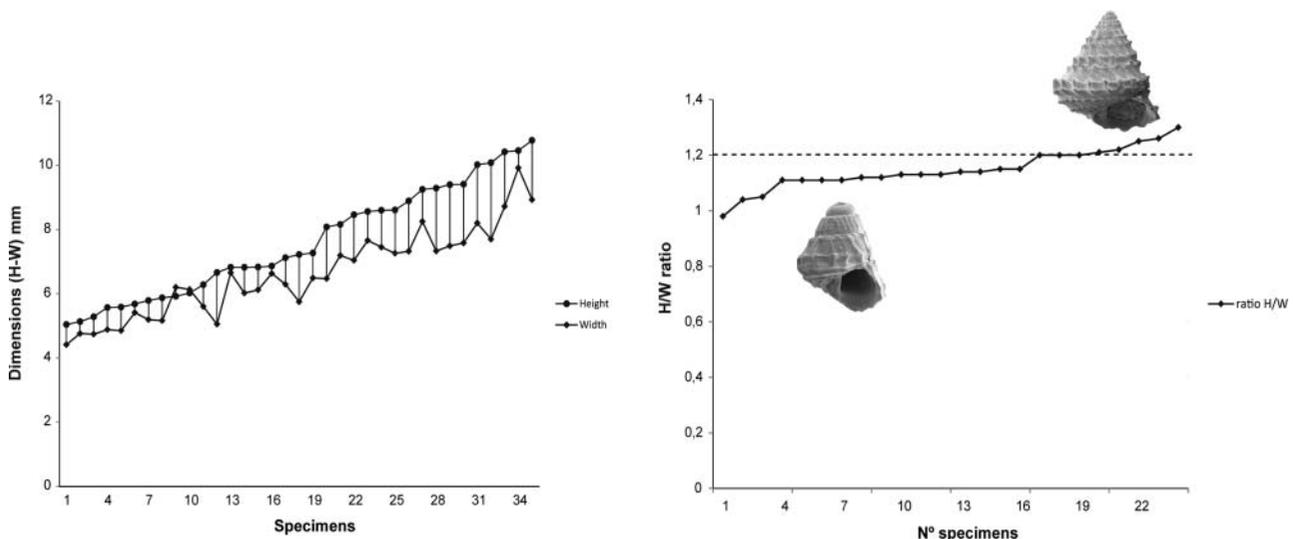
Figure 4. Relationships between the H/W ratio in juvenile and adult specimens of *Calliotropis* (*R.*) *biarmata* (Münster).

prosocline and crowded growth lines are visible on mature whorls and on the base. Base slightly convex to flattened, ornamented by three strongly nodular spiral cords. Juvenile specimens have a quadrangular aperture, prosocline, slightly inclined with respect to the coiling axis, and a visible pseudoumbilicus. Adult specimens have an holostomatous and circular to sub-circular aperture with the peristome continuous; the outer lip is indented by external ornament and the columellar lip thickened as a moon-shaped callus which covers the pseudoumbilical area. The outer rim of the columellar callus forms an acute outer ridge which gives the callus a concave appearance; this character is absent in juvenile specimens.

Dimensions. See Supplemental Table 3.

Remarks. This species was described in detail by Conti & Monari (2001) as *Riselloidea biarmata* (Münster, 1844), and subsequently assigned by Kaim (2004) to *Calliotropis*. Kaim (2004) recognized *Calliotropis* (*Riselloidea*) *bitorquata* (Hébert & Eudes-Deslongchamps, 1860) and *Calliotropis* (*Riselloidea*) *sauvagei* (Cossmann, 1895) as varieties of one highly variable species. *Calliotropis* (*Riselloidea*) *naybandensis* (Nützel & Senowbari-Daryan, 1999, p. 1000, pl. 1, figs 7–9, pl. 7, figs 4, 5), from the Upper Triassic (Norian–Rhaetian) of Central Iran, differs from *C.* (*R.*) *biarmata* in having three primary spiral cords on the outer face of the whorls, a slightly larger shell, and more nodular elements on the base. *Calliotropis* (*Riselloidea*) *aliabadensis* (Nützel & Senowbari-Daryan, 1999, p. 101, pl. 1, figs 10, 11, pl. 7, figs 1–3), the type species of *Trochonodus* Nützel *et al.*, 2003 from the Upper Triassic of Iran, differs from *C.* (*R.*) *biarmata* in having a median spiral cord on the outer face of the whorls, more rounded nodes on the base, and a rounded sub-quadrangular aperture. *Calliotropis* (*Riselloidea*) *pileiformis* (Jaitly *et al.*, 2000, p. 56, pl. 5, figs 15, 16, pl. 6, figs 1–3), from the Middle Jurassic (Bathonian) of India, differs from *Calliotropis* (*R.*) *biarmata* in being slightly larger, having a rather wide C-shaped callus extending from the columellar lip to the first basal cord, a wider spiral angle, and a double subsutural carina. *Calliotropis* (*Riselloidea*) *vierowiensis* Gründel, 2000 (p. 229, pl. 6, figs 16, 17; Gründel 2003b, p. 153, pl. 5, figs 6, 7), from the Middle Jurassic (Callovian) of Germany, has secondary spiral cords on the ramp of the whorls, more rounded nodes at the peripheral keel, the base is slightly convex and ornamented by more than 15 spiral furrows, and a pseudoumbilicus is lacking.

Calliotropis (*Riselloidea*) *faustiankensis* sp. nov.
(Figs 3K–N, 5A–L)

?2004 *Eucycloscala* sp. 2 Kaim: p. 19, fig. 7A, B.

Diagnosis. Shell conical to slightly coeloconical; protoconch of 0.25 mm width, dome-shaped, paucispiral, clearly demarcated, sculptured with numerous pits forming a net-like pattern, somewhat microhexagonal, consisting of 1.5 whorls; strong axial ribs dominate at juvenile whorls; later in ontogeny whorls angulate at two keels; pointed and acute nodes at the spiral keels on mature whorls; a third secondary and weakly developed spiral cord emerging from suture at third whorl; strongly prosocline growth lines visible on later whorls; dotted micro-ornament; base convex to flattened, sculptured by three nodular spirals; aperture quadrangular on juvenile shells and sub-circular on adult specimens, with the columellar lip thickened as a moon-shaped callus; very narrow umbilicus.

Derivation of name. In reference to the Faustianka locality, where the material was found.

Material. Holotype: ZPAL. Ga. 18/36. Paratypes: ZPAL. Ga. 18/37, Ga. 18/38. Faustianka locality, Częstochowa region (Fig. 2), Poland, Jurassic, Middle Bathonian.

Description. Dextral, trochiform, conical, cyrtoconoid on earliest whorls and conical to coeloconoid toward mature growth stages. Protoconch dome-shaped, symmetrically paucispiral, consisting of 1.5 bulbous, convex whorls, with a width of 0.25 mm, sculptured by small, irregular, somewhat microhexagonal granules that connect to form net-like pattern more clearly visible on the adapical and abaxial margin (Fig. 5C). Clear demarcation between protoconch and teleoconch. Teleoconch consisting of 5 whorls, with a mean height of 2.9 mm and a mean width of 2.8 mm. The spire angle is 75° and the basal angle 97°. Sutures impressed on a concave spiral furrow. First teleoconch whorl strongly convex and ornamented by 21 strong orthocline to slightly prosocline ribs which run from suture to suture. At the second whorl, an adapical and very weak spiral cord appears near the suture, forming small nodes at the intersection with the strong axial ribs. On the third whorl, a third abapical spiral cord emerges weakly from the suture. From the third whorl to mature growth stages the shell is strongly conical with a flattened ramp and very narrowly developed outer face. The ramp of the shell becomes slightly concave towards the mature whorls. Axial ribs are weakly visible on the third whorl and become obsolete on mature whorls. The periphery of the whorls is marked by a nodular spiral keel; a second adapical and nodular keel borders the suture in the upper portion of the ramp. The distance between the two keels is large. The third spiral cord is completely visible on last whorl. Nodes are slightly stronger on the peripheral keel and number 23. On the adapical spiral cord nodes number 19. Nodes on the sutural cord are upwardly curved, and on the peripheral keel horizontally oriented. The shell surface is ornamented by a dotted micro-ornament. Base strongly convex, ornamented by 4–5 spiral cords. Near the umbilical area, the spiral cords have separated and rounded nodes. Weak and crowded orthocline growth
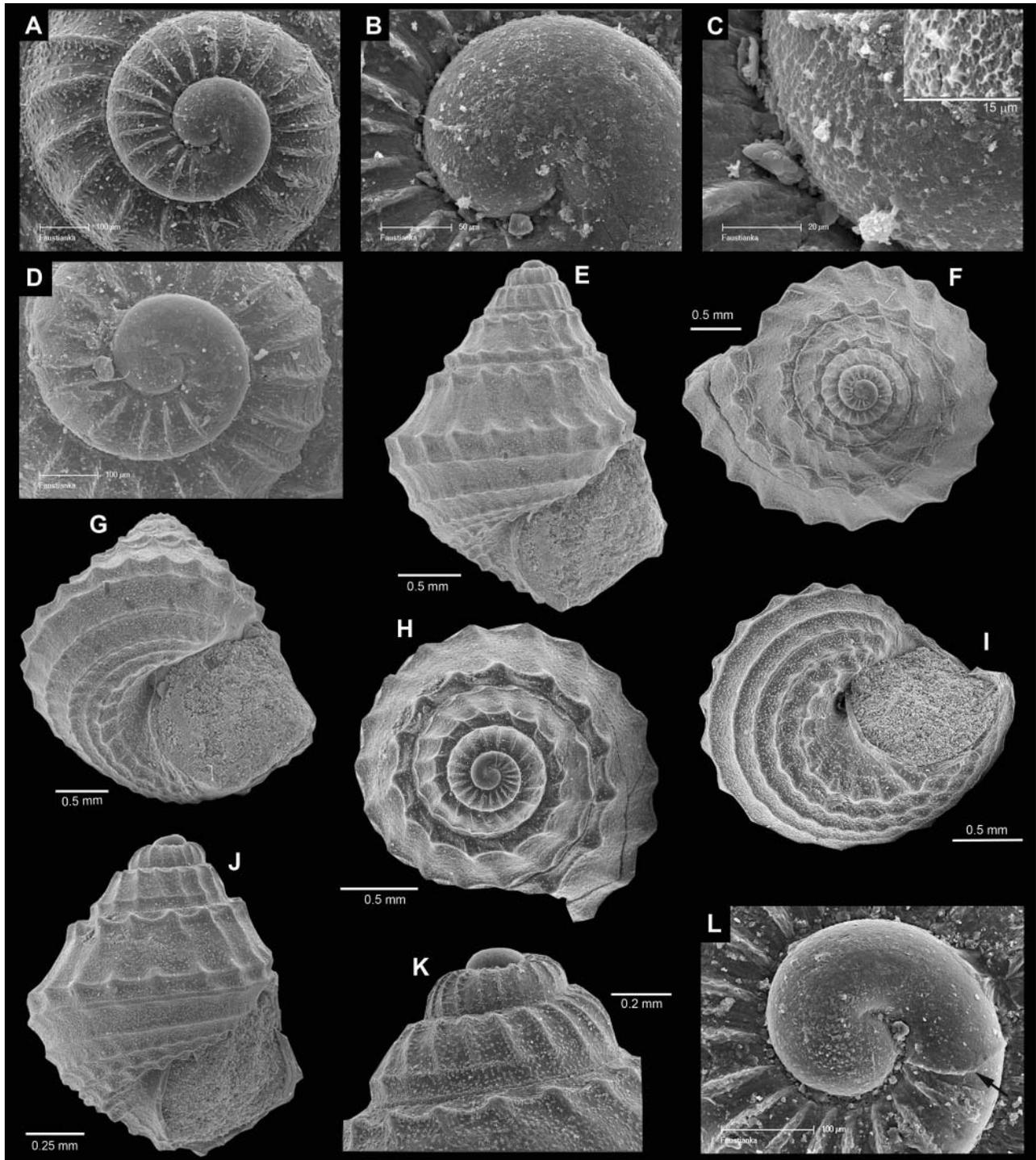
Figure 5. *Calliotropis* (*Riselloidea*) *faustiankensis* sp. nov., Middle Bathonian, Faustianka, Poland. **A–C, K,** holotype, ZPAL.Ga.18/36; **A,** protoconch and earliest teleoconch whorls in apical view; **B,** protoconch detail; **C,** protoconch ornament detail showing a net-like pattern; **K,** protoconch and earliest teleoconch whorls in lateral view. **D–G,** paratype, ZPAL.Ga. 18/37; **D,** protoconch and first teleoconch whorls detail; **E,** lateral view; **F,** apical view; **G,** basal and apertural views. **H–J, L,** paratype, ZPAL. Ga. 18/38; **H,** apical view; **I,** basal, apertural and umbilical detail; **J,** lateral view; **L,** protoconch detail, arrow showing clear demarcation between protoconch and first teleoconch whorl.

lines intercept the spiral cords on the base. The aperture is subcircular; the outer lip thickened, indented by external spiral cords. Columella prosocline and thickened. A very narrow, deep and funnel-shaped umbilicus is clearly visible, with a diameter measuring 8.75% of the shell width.

Dimensions. See Supplemental Table 4.

Remarks. Regarding Middle Jurassic *Calliotropis* species, *Calliotropis* (*R.*) *biarmata* differs from *C.* (*R.*) *faustiankensis* sp. nov. in lacking a funnel-shaped and narrow umbilicus and the dotted micro-ornament, in having a more acute spire angle and a wider basal angle, a wider protoconch, slightly smaller shell, and more conspicuous nodes on the shell surface and the base. *Calliotropis* (*R.*) *lorioli* (Greppin, 1898), from the Bajocian of Germany, differs from *C.* (*R.*) *faustiankensis* sp. nov. in having three primary and nodular spiral keels on the outer face of the whorls, more rounded nodes, a base with 2−3 spiral keels, the inner lip forming a broad columellar callus, and lacks an umbilicus (Gründel 2003a, p. 65, pl. 6, figs 9, 10). *Calliotropis* (*R.*) *faustiankensis* sp. nov. is very similar to *Calliotropis* (*R.*) *keideli* Ferrari *et al*., 2014, from the Early Jurassic of Argentina; however, *C.* (*R.*) *faustiankensis* sp. nov. has a much larger distance between the two spiral cords, and has a strongly dotted micro-ornament over the whole shell surface, while in the Argentinean form it seems to consist of enhanced growth lines.

Calliotropis (*R.*) *faustiankensis* sp. nov. shares a similar protoconch ornament with extant vetigastropods of the families Calliostomatidae, Scissurellidae and Skeneidae, and fossil Calliotropidae and Seguenzoidea. For instance, *Calliostoma* (*Fautor*) *consobrina* (Powell, 1958) (see Marshall 1979, p. 538, fig. 7M–O) and *Calliostoma* (*Tristrichotrochus*) *gendalli* (Marshall 1979, p. 538, fig. 7I–L), both from the Holocene of New Zealand, have a characteristic protoconch sculptured by thin-walled microhexagons. This pattern is also present in the extant scissurellid *Satondella tabulata* (see Geiger *et al*. 2008, p. 301, fig. 12.2.O), in the skeined *Pondorbis japonicus* Habe & Ando, 1980 (see Sasaki 1998), in the fossil calliotropid *Calliomphalus paucispirilus* Sohl, 1964 (see Bandel 2010, p. 474, fig. 14F–I) and in the seguenzioidean *Adeuomphalus ammoniformis* Seguenza, 1876 (see Kano *et al*. 2009).

Calliotropis (*Riselloidea*) *lukovensis* sp. nov.
(Fig. 6A–L)

2004 *Calliotropis* sp. Kaim: p. 24, fig. 10.

Diagnosis. Protoconch of 0.3 mm width, dome-shaped, paucispiral, clearly demarcated, sculptured with numerous pits forming a net-like pattern, roughly microhexagonal, consisting of 1.5 whorls; first teleoconch whorl with fine and weak collabral threads; axial ribs lacking at second whorl; two weak abapical spiral cords at second whorl; 1−2 additional spiral cords appear on mature whorls; base with five acute spiral cords; juvenile shell with quadrangular aperture; adult shell with sub-circular aperture; pseudoumbilicus present.

Derivation of name. In reference to Łuków, where the material was found.

Material. Holotype: ZPAL. Ga. 18/39. Paratype: ZPAL. Ga. 18/40. Additional material: two juvenile specimens (ZPAL Ga. 18/41–42). Łuków, Podlasie (Fig. 2), Poland, Jurassic, Middle Callovian).

Description. Dextral, small-sized, trochiform, cyrto-conical in earliest whorls to slightly coeloconical towards mature growth stages, and moderately high-spired shell. Protoconch dome-shaped, symmetrically paucispiral, strongly convex and consisting of 1.5 whorls with a width of 0.3 mm, sculptured by small, irregular, somewhat microhexagonal granules that connect to form a net-like pattern more clearly visible on the adapical and abaxial margins (Fig. 6G). Clear demarcation between protoconch and teleoconch. Teleoconch of adults consists of 7 whorls, with a spire angle of 66° and a basal angle of 90°. Sutures impressed in a concave spiral furrow. First teleoconch whorl strongly convex starting with fine and weak collabral lines; on second whorl, axial ribs are lacking; collabral lines are visible and intercept two fine regularly spaced spiral cords; the abapical spiral cord is stronger than the adapical. The third teleoconch whorl becomes less convex and more coeloconoid. Axial ribs appear from third whorl and are stronger towards mature growth stages, and along all teleoconch whorls. The two abapical spiral cords are also visible from the third teleoconch whorl, and an adapical cord appears bordering the sutures. Rounded and pointed nodes are visible at the intersection of axial and spiral elements from third whorl. On the fifth teleoconch whorl the two abapical spiral cords are completely visible and more or less equally developed. The peripheral abapical spiral cord bears stronger and more pointed nodes than the secondary spiral cord. Towards mature whorls 1 to 2 additional secondary spiral cords appear on the flanks of whorls, closer to the primary abapical spiral cord. Nodes are still weaker at the crossing points of secondary cords and axial ribs. Nodes number 15 on earliest whorls and remain more or less constant (16) on mature whorls. Strongly prosocline and crowded growth lines cover the shell surface and the base. The base is slightly convex to flat and ornamented with 5 acute spiral cords which are smooth in juvenile specimens and ornamented with small and rounded nodes in adults. The spiral elements are intercepted by fine, prosocline and crowded collabral growth lines (Fig. 6E). In juveniles, the aperture is holostomatous and
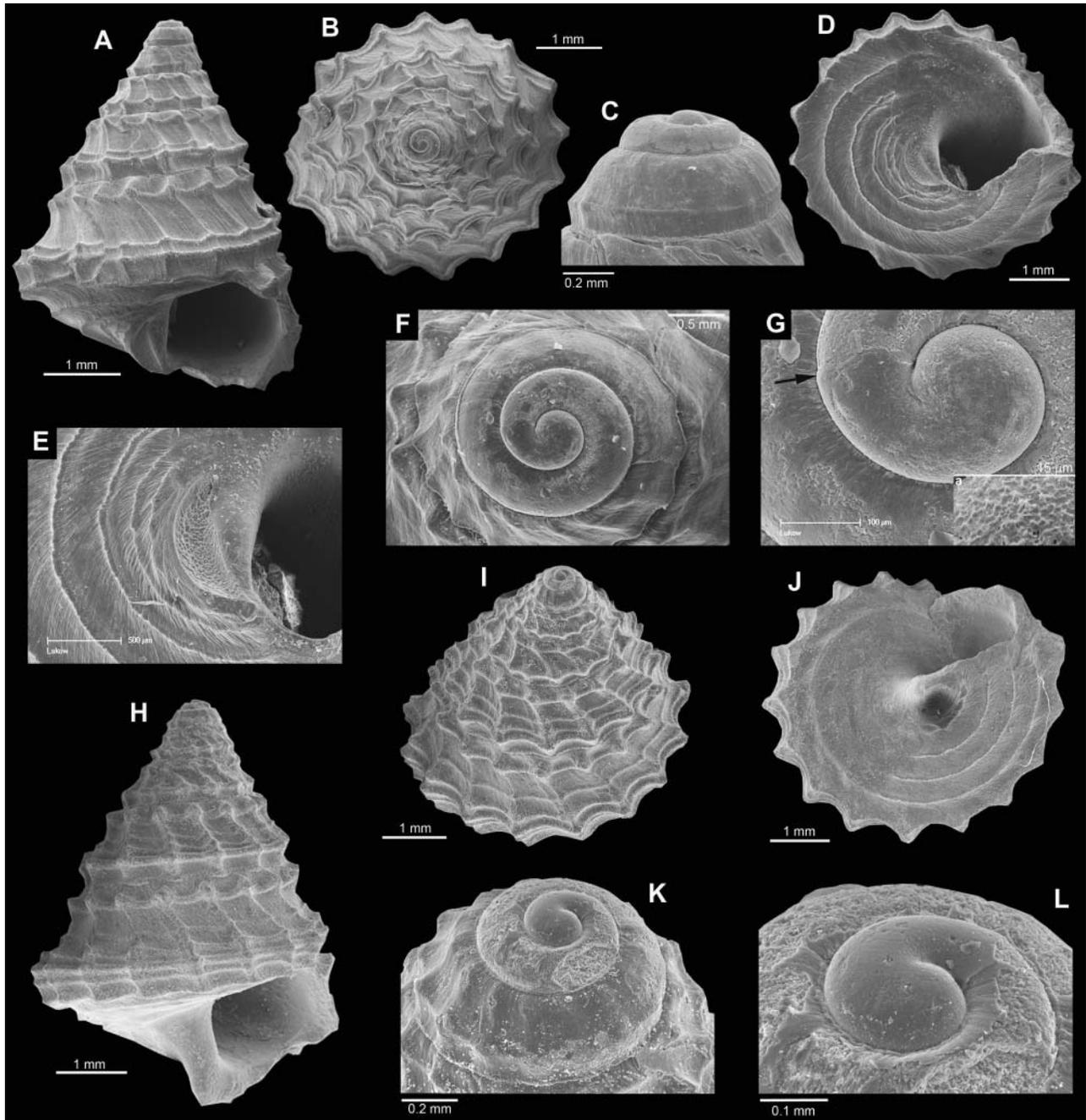
Figure 6. *Calliotropis* (*Riselloidea*) *lukovensis* sp. nov., Middle Callovian, Łuków, Poland. **A–G,** holotype, ZPAL. Ga. 18/39; **A,** lateral view; **B,** apical view; **C,** protoconch and earliest teleoconch whorls in lateral view; **D,** basal and apertural views; **E,** pseudoumbilical area detail; **F,** protoconch and earliest teleoconch whorls in apical view; **G,** protoconch detail showing the net-like ornament sculpture (a) with arrow showing clear demarcation between protoconch and teleoconch. **H–L,** paratype, ZPAL. Ga. 18/40; **H,** lateral view; **I,** apical view; **J,** basal and pseudoumbilical view; **K,** protoconch and earliest teleoconch whorls in apical view; **L,** protoconch detail.

quadrangular, slightly inclined respect the coiling axis; the peristome is continuous with the outer lip, not indented by external ornament and the pseudoumbilicus is visible. In adults, the aperture is subcircular with the outer lip not indented by external ornament and the columellar lip thickened as a callus which covers the pseudoumbilicus.

Dimensions. See Supplemental Table 5.

Remarks. The new species here described fits with the characterization of *Calliotropis*, having a conical shell with a convex and smooth protoconch, an adult shell with two primary nodular keels, axial ribs visible on the shell surface, a convex base and a pseudoumbilicus. The lack

of axial ribs on the second whorl, the appearance of secondary additional spiral cords in mature growth stages and the base ornamented by acute smooth spiral cords separates *C.* (*R.*) *lukovensis* sp. nov. from other species of the genus.

Calliotropis (*R.*) *biarmata* differs from the new species in having strong axial ribs on the first teleoconch whorl, lacking secondary spiral cords on mature whorls, and having the base sculptured by three strongly nodular spiral cords. *Calliotropis* (*R.*) *faustiankensis* sp. nov. is much smaller, has a slightly narrower umbilicus, a more convex base with nodular spiral cords, strong axial and regularly spaced ribs on the first teleoconch whorl, less pointed nodes on the primary abapical and adapical spiral cords, lacks secondary spiral cords on the flanks of mature whorls, and has a dotted micro-ornament over the whole shell surface. *Calliotropis* (*Riselloidea*) *pileiformis* Jaitly *et al*., 2000, p. 56, pl. 5, figs 15, 16, pl. 6, figs 1–3), from the Middle Jurassic (Bathonian) of India, differs from *C.* (*R.*) *lukovensis* sp. nov. in being larger, having the adapical keel divided into two spiral keels from the third teleoconch whorl, and a flattened base ornamented by four strongly nodular spiral keels. *Calliotropis* (*Riselloidea*) *multistriata* (Böckh, 1874) (see Szabó 1982 (p. 25, pl. 3, figs 3–6), 2009 (p. 82, fig. 77)), from the Early Jurassic (upper Sinemurian–lower Pliensbachian) of Hungary, is similar to the Polish species; however, the Hungarian form has a more convex surface, nodes at the intersection points of spiral and axial elements are smaller and more rounded, a more convex base ornamented by several and regularly spaced spiral cords, a sub-circular aperture, and a wider pseudoumbilical area. *Calliotropis* (*Riselloidea*) *noszkyi* Szabó, 1995 (p. 71, pl. 7, fig. 13; 2009, p. 83, fig. 78), from the Early Jurassic of Hungary, is also comparable to *Calliotropis* (*R.*) *lukovensis* sp. nov. but *Calliotropis* (*R.*) *noszkyi* has strongly convex teleoconch whorls and an anomphalous base. *Calliotropis* (*Riselloidea*) *lorioli* (Greppin, 1898) (as *Biarmatoidela lorioli* in Gründel 2003a, p. 65, pl. 6, figs 9, 10), from the Middle Jurassic (Bajocian) of Germany, differs from *Calliotropis* (*R.*) *lukovensis* sp. nov. in having three strongly nodular spiral keels on the outer face of the whorls, nodes which are more rounded at the intersections of spiral and collabral elements, growth lines strongly prosocline, a base that is flattened and anomphalous, and the inner lip forming a broad columellar callus.

Shell functional morphology

As molluscs grow, they enlarge their shells and record in them details of the everyday events which marked their lives. Thus, shells are functional structures whose form reflects the way in which the animals that build these shells are adapted to and limited by their surroundings (Vermeij 1993). Gastropods tend to adapt their shell morphology in response to the environment in which they live. For instance, gross features such as spire angle, umbilicus size and apertural orientation affect the position of the centre of gravity of the shell, determine how the shell interacts with the fluid environment, and how water may flow within the shells. Consequently, functional and ecomorphological interpretations of extant and fossil gastropods have to consider these features. Wagner & Erwin (2006) examined evolutionary patterns among four general shell features, comprising spire angle, basal angle, umbilicus width and apertural inclination. These features are amalgamations of multiple independent shell characters, but they have an advantage over more minute details as in most cases they can be measured exactly. Moreover, these characters vary within species and also within individuals over ontogeny, and thus, functional and taxonomic interpretations may rely on these features. The spire angle reflects coiling parameters, and the general shape and orientation of the aperture. Spire angle affects functional interpretations such as ease of mobility, orientation on the substrate, and resistance to breakage. The umbilicus is a depression on the base in which earlier whorls are exposed. Parts of the shell in the vicinity of the umbilicus are unsupported by previous whorls and therefore umbilicate shells are weaker constructionally and more susceptible to breakage (Vermeij 1977, 1987, 1993). Geographical and ecological distributions of umbilicate shells seem to confirm the idea that umbilicate coiling incorporates structural weakness (Vermeij 1993). Umbilicus size also affects the centre of shell gravity and ease of locomotion, shells with a large umbilicus being more difficult to carry than similar shells with a small umbilicus (Linsley 1978). The basal angle reflects the shape of the base. The presence of a siphonal notch creates a very low basal angle. A flat or nearly flat base might reflect a sedentary habit on a soft substrate. The apertural inclination strongly affects how the snail carries the shell (with inclined apertures encouraging balancing of the shell over the gastropod foot) and thus affects animal mobility (Linsley 1977, 1978).

Vermeij (1993) also suggested that shell shape and sculpture influence the heat budget of the snail and that mortality from heat and desiccation increases in upper shoreface or coastal marine environments. Sun-exposed gastropods tend to develop high-spired, conical shells sculptured by spiral cords, nodes or tubercles. Conical shells bear the spire pointing in the direction of the sun, so a sun-exposed gastropod in its natural orientation decreases the absorption of the sun rays. The developed sculpture characteristic of most sun-exposed, upper shoreface gastropods creates a large surface area from which heat can be radiated. In contrast, species occurring on the

lower shoreface are almost always lower-spired than their higher-spired shallower counterparts and have smooth to finely ribbed or weakly granular textures. Moreover, gastropods living in coastal marine environments and rocky shores are frequently exposed to strong flows, waves and powerful currents, and all these forces must be resisted by shell architecture. In contrast, small size and lack of the umbilicus facilitate resistance to strong forces in flow. Powerful currents have a relatively greater impact on large and umbilicated shells than on small and non-umbilicated shells, and low spires also confer high stability under these conditions.

Results

Cluster and principal component analyses were performed in an attempt to infer the relationships of extinct and living *Calliotropis* and highlight the pattern of evolution of some functional and ecomorphological characters of these

gastropods. The cluster analysis found two discernible morphological types for the genus *Calliotropis* which partly correlate with the two subgenera distinguished by Ferrari *et al.* (2014), i.e. *Calliotropis* (*Riselloidea*) and *Calliotropis* (*Calliotropis*) (Fig. 7).

Group A unites shallow-reef ecophenotypes and includes 21 *Calliotropis* species, predominantly belonging the subgenus *Calliotropis* (*Riselloidea*), where the most basal and primitive morphologies are represented, including the type species of *Riselloidea*, *Calliotropis* (*R.*) *subdisjuncta* (Fig. 7). The most ancient species reported from the Upper Triassic of Iran belong to this group and these are *Calliotropis* (*R.*) *naybandensis*, *Calliotropis* (*R.*) *aliabadensis* and *Calliotropis* (*R.*) *iranicus*. *Calliotropis* (*R.*) *antarchais* has been interpreted by Stilwell (2005) as a basal member of the genus and in the present analysis it is also present within the ancient group. Stilwell (2005) suggested that retention of the strongly and coarsely reticulate shell sculpture throughout ontogeny is a basal condition within *Calliotropis*, whereas it is much reduced or absent
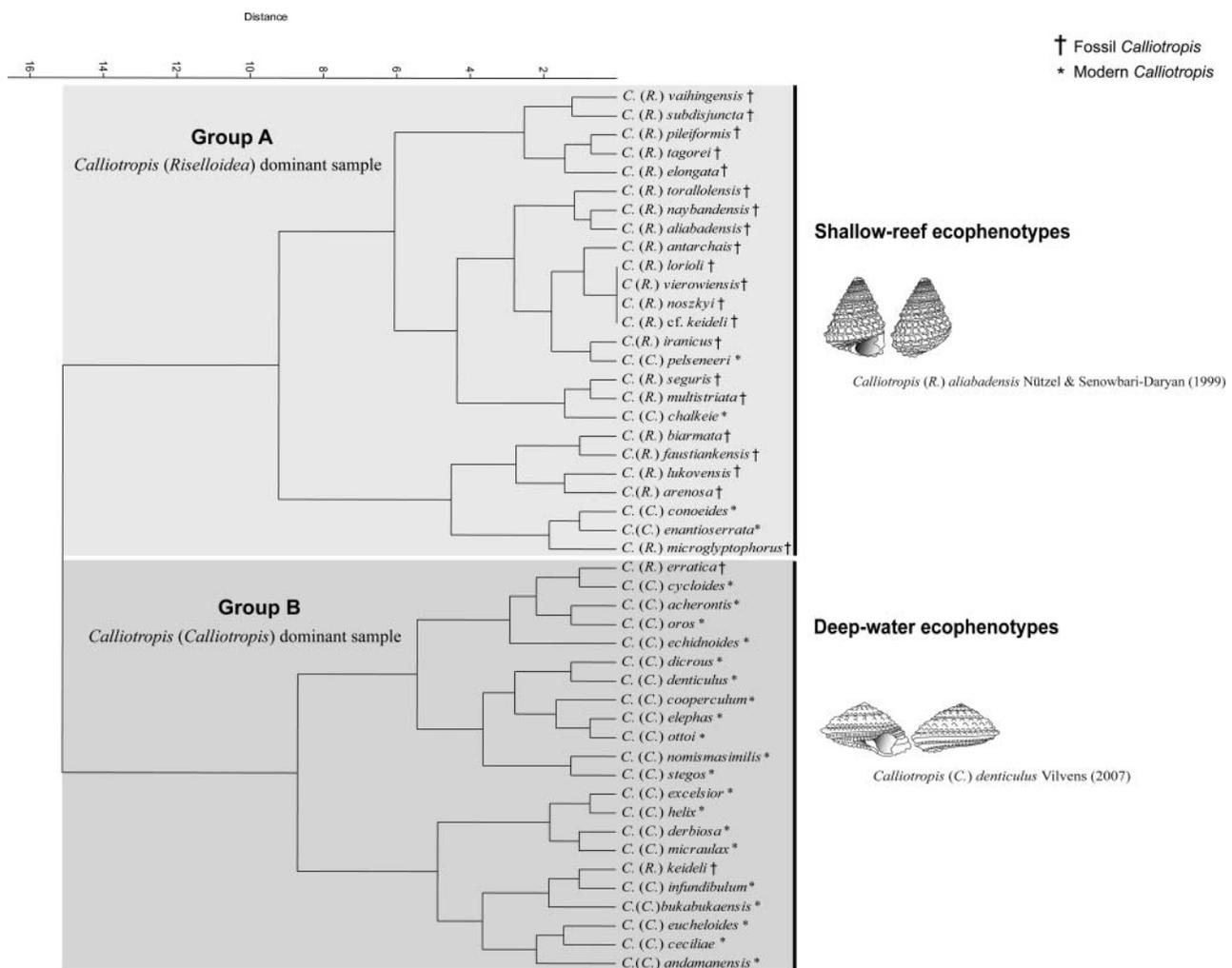
Figure 7. Cluster analysis using Ward's algorithm. Note good clustering between the shallow-reef ecophenotypes (Group A) compared to the deep-water ecophenotypes (Group B).

in extant forms. Most of the *Calliotropis* species within Group A – *Calliotropis* (*R.*) *naybandensis*, *Calliotropis* (*R.*) *aliabadensis*, *Calliotropis* (*R.*) *iranicus*, *Calliotropis* (*R.*) *vaihingensis*, *Calliotropis* (*R.*) *noszkyi*, *Calliotropis* (*R.*) *lorioli*, *Calliotropis* (*R.*) *pileiformis*, *Calliotropis* (*R.*) *vierowiensis*, *Calliotropis* (*R.*) *lukovensis*, *Calliotropis* (*R.*) *torallolensis*, *Calliotropis* (*R.*) *microglyptophorus* and *Calliotropis* (*R.*) *antarchais* – have a strong and reticulate ornament pattern consisting of two or three primary spiral cords plus additional secondary spiral cords visible towards mature growth stages which are generally intercepted by axial ribs forming conspicuous and/or spinose nodes at the crossing points. The species within this group also lack a widely open umbilicus or have a very narrow umbilical chink or pseudoumbilicus. They share a spire angle $\leq 95°$, grouping high- to moderately high-spired shells which is indicated by the presence of a H/W ratio >1 (see Supplemental Table 1). Species within Group A also have medium-sized shells, with a height between 6 and 15 mm, except for *Calliotropis* (*R.*) *arenosa* and *Calliotropis* (*R.*) *faustiankensis* sp. nov. which have very small shells (H < 6 mm). Protoconchs are very small and show a microgranular ornament pattern, although protoconchs are usually unknown from the extinct species of *Calliotropis*.

Group B unites deep-water ecophenotypes of *Calliotropis*, predominantly species of the subgenus *Calliotropis* (*Calliotropis*). The majority of living *Calliotropis* species belong to Group B, e.g. the type species *Calliotopis* (*C.*) *ottoi* (Fig. 7), *Calliotropis* (*C.*) *excelsior*, *Calliotropis* (*C.*) *helix*, *Calliotropis* (*C.*) *dicrous*, *Calliotropis* (*C.*) *elephas*, *Calliotropis* (*C.*) *infundibulum*, *Calliotropis* (*C.*) *ceciliae*, *Calliotropis* (*C.*) *oros*, *Calliotropis* (*C.*) *nomismasimilis*, *Calliotropis* (*C.*) *andamanensis* and *Calliotropis* (*C.*) *bukabukaensis*. These forms show a simpler and less reticulate ornament pattern, in which the third or fourth strong spiral cord is infrequent on mature whorls, and nodes are generally smaller, rounded and less conspicuous and not spinose (cf. fossil forms). The modern group usually shows a widely opened and funnel-shaped umbilicus, and spire angle is variable, although some species such as *Calliotropis* (*C.*) *oros*, *Calliotropis* (*C.*) *denticulus*, *Calliotropis* (*C.*) *stegos* and *Calliotropis* (*C.*) *nomismasimilis* have a nearly flat top with a spire angle > 100°. The former character is completely missing in extinct *Calliotropis*. The flat top is also revealed by the presence of a depressed spire with an H/W ratio < 0.7. Within Group B, very large shells (H > 15 mm) and very small shells (H < 6 mm) are common, while medium-sized (H = 6–15 mm) shells are rare but more frequent in the ancient group. The protoconch of living calliotropids is generally more bulbous than those of fossil species, and smooth or glassy. There are, however, some fossil calliotropids that share features with the living species and belong to Group B, e.g. *Calliotropis* (*R.*) *erratica* and *Calliotropis* (*R.*) *keideli*. These

forms have a more or less open umbilicus and lack several secondary spiral cords towards the mature teleoconch whorls. On the other hand, the extant *Calliotropis* (*C.*) *conoeides*, *Calliotropis* (*C.*) *pelseneeri*, *Calliotropis* (*C.*) *chalkeie* and *Calliotropis* (*C.*) *enantioserrata* belong to the group dominated by fossil calliotropids. This may be related to the absence of an umbilicus in some of the species (e.g. *C.* (*C.*) *conoeides*, *C.* (*C.*) *pelseneeri* and *Calliotropis* (*C.*) *enantioserrata*), the strongly reticulate ornament with several secondary spiral cords on the shell surface and towards the mature whorls (e.g. *C.* (*C.*) *pelseneeri*), and the presence of conspicuous and spinose nodes (e.g. *Calliotropis* (*C.*) *chalkeie*). Finally, features such as basal angle and apertural inclination did not show significant differences between extinct and modern species of *Calliotropis*.

We also performed a principal component analysis (PCA) to depict the results obtained from the cluster analysis and to show the differences in shell morphology between shallow reef and deep-water ecophenotypes in species of *Calliotropis* (Fig. 8A, B). When species are plotted according to the two major groups identified a posteriori with the cluster analysis, most of the species of Group A are on the left side of the ordination and most of species of Group B are on the right side. This is especially true when two outliers – *C* (*C.*) *pelseneeri* and *C.* (*R.*) *erratica* – are excluded from the dataset (Fig. 8B). *Calliotropis* (*C.*) *pelseneeri* is a living species and displays 'shallow-water' shell morphologies, while *C.* (*R.*) *erratica* is a Jurassic form and displays 'deep-water' shell characteristics, thus highlighting the complexity of the problem and difficulty in classifying these taxa (Fig. 8B).

Shallow-reef ecophenotypes belonging to Group A (*Calliotropis* (*Riselloidea*) species) are on the left side of the ordination, sharing morphological characters such as a lower spire angle and a very narrow or absent umbilicus (Fig. 8B). In contrast, deep-water taxa belonging to Group B (*Calliotropis* (*Calliotropis*) species) are on the right side of the ordination and are characterized by a high spire angle and a moderately wide to very wide umbilicus (Fig. 8B).

Discussion

The set of shell characters that distinguish the two groups of *Calliotropis* may be preliminarily considered as a response to environmental conditions, with ecophenotypic variation translated into evolutionary change. As pointed out by Ferrari *et al.* (2014), extant calliotropids are abundant, diverse and widely distributed gastropods. Their adaptational abilities are also apparent from the wide range of their bathymetrical occurrences. Nevertheless, they are most common in the deep sea, ranging from a few hundred metres to more than 3200 m (Vilvens 2007) (see Supplemental Table 1). Hickman & McLean (1990),
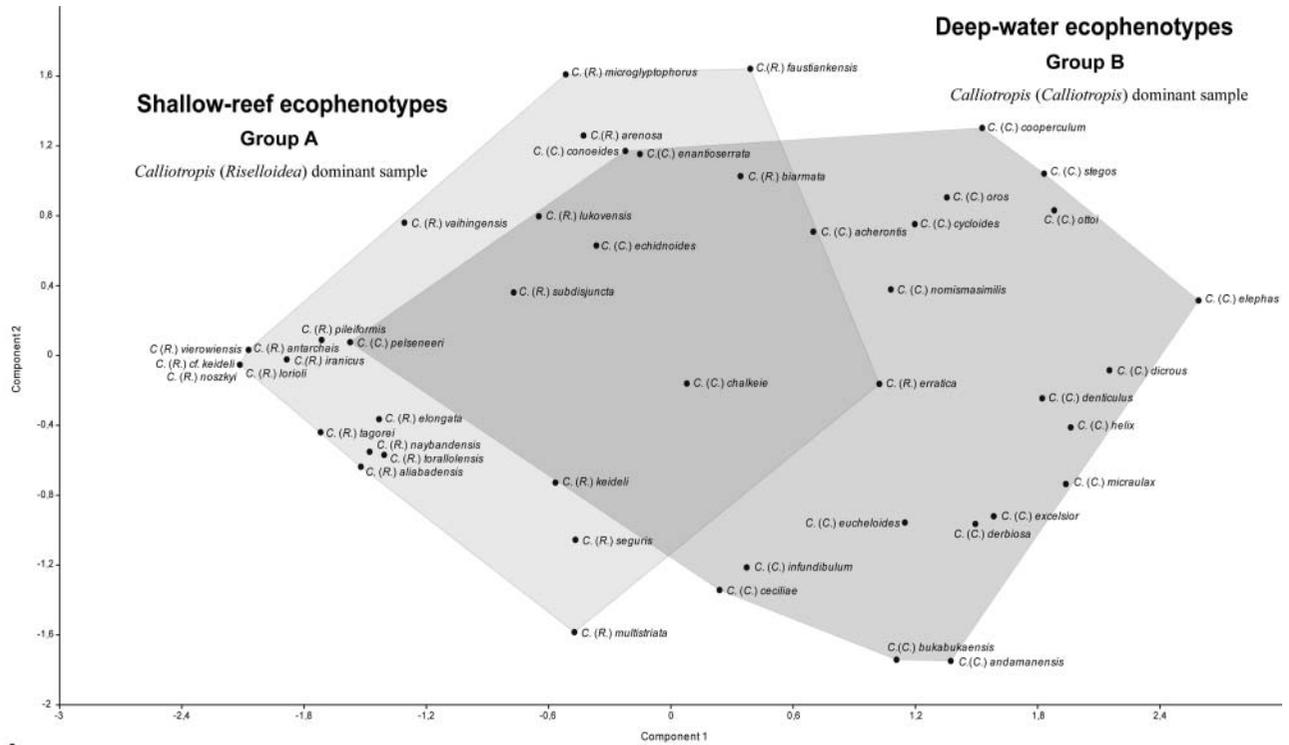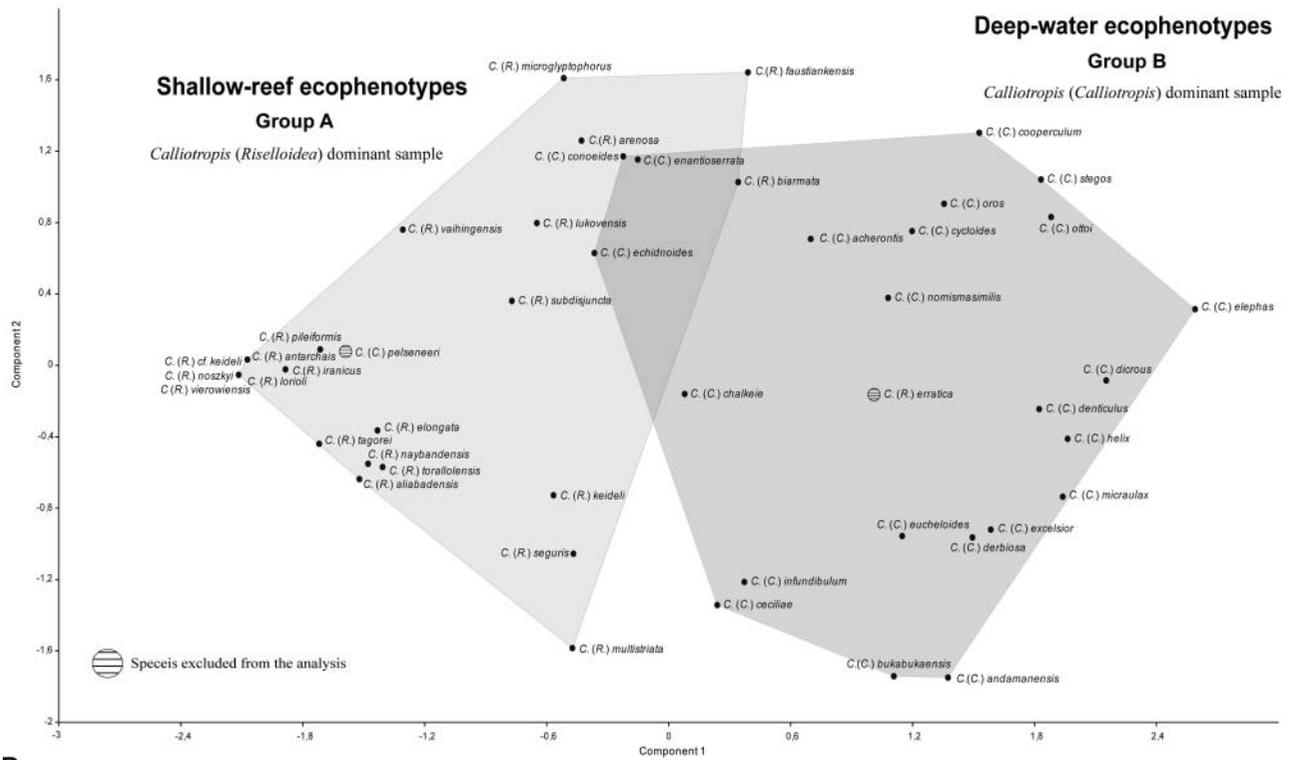
Figure 8. Principal component analysis showing the differences in shell morphology between shallow-reef and deep-water ecophenotypes of the species of *Calliotropis*. **A,** including all *Calliotropis* species; **B,** excluding *C* (*C.*) *pelseneeri* and *C* (*R.*) *erratica*, which clearly deviate from the described pattern.

Szabó (1995) and Hickman (2016) have also argued that living calliotropids occur predominantly in bathyal (> 200 m) to abyssal depths in offshore regions on fine-grained unconsolidated sediments, and they seem to be adapted to cool and cold waters, their individuals sometimes locally dominating slope communities. In contrast to living species, Mesozoic species of *Calliotropis* were more common in shallow marine environments, where agitated waters prevailed. Hickman & McLean (1990) found the highest abundance of fossil calliotropids in Tethyan shallow waters and in reef-associated palaeoenvironments as their data seem to have been mainly collected from facies of Western European epicontinental seas. However, during Holocene times species of *Calliotropis* are mostly deep-water forms, suggesting a Cenozoic shift from the shallow-water environments into bathyal depths.

As stated above, fossil calliotropids are predominantly defined by a set of shell characters, which include a strongly reticulate ornament consisting of 2 or 3 primary spiral cords plus several additional secondary spiral cords appearing towards mature growth stages and generally intercepted by axial ribs forming conspicuous and/or spinose nodes at the crossing points. The majority of ancient *Calliotropis* species also lack a widely open umbilicus, and they have high- to moderately high-spired and medium- to small-sized shells. In coastal, upper shoreface and shallow marine environments the strongly developed sculpture, high-spired shell, and medium- to rather small-size may have been constructional response to the solar radiation and the strong forces of flows, waves and powerful currents. The reduction of the umbilicus may also have been related to making the shells more resistant to breakage in shallow marine environments where agitated waters and powerful currents prevailed (Fig. 9). In contrast, living members of *Calliotropis* are strikingly more diverse in morphology, although generally characterized by the presence of a simpler and less reticulate sculpture in which nodes are smaller, rounded and less conspicuous and spinose. They usually show a widely open and funnel-shaped umbilicus, and shells have a nearly flat top and depressed spire, while very small shells are commonly present. These architectural constraints seem to prevail in lower shoreface habitats and bathyal to abyssal depth environments where cool and cold waters prevail and solar radiation and strong current flow does not produce a negative impact on the benthic marine gastropod communities as in shallow marine environments (Fig. 9). The large shells of some living species of *Calliotropis* (*Calliotropis* (*C.*) *ceciliae*, *Calliotropis* (*C.*) *derbiosa*, *Calliotropis* (*C.*) *excelsior*, *Calliotropis* (*C.*) *conoeides* and *Calliotropis* (*C.*) *enantioserrata*) inhabiting depths of more than 1100 m could have been developed to deter manipulation by predators. Jablonski & Bottjer (1990) suggested that the expansion of predators and competitors capable of active displacements could drive older clades offshore, making deep water a refuge for species with poorly developed competitive and defensive capacities. This is particularly related to the growing predation pressure in shallow water environments which started with the advent of neogastropods in the Early Cretaceous.

Jablonski & Bottjer (1990) documented patterns of first occurrences along marine environmental gradients and suggested that a variety of taxa today restricted to deep-water shelf environments can be inferred on functional or palaeontological grounds to have originated in shallow-water settings, reporting onshore origination of major benthic communities. They supported the idea that bathymetric gradients such as temperature, salinity, turbidity, disturbance and spatial heterogeneity influence biotic factors including population densities and persistence, life
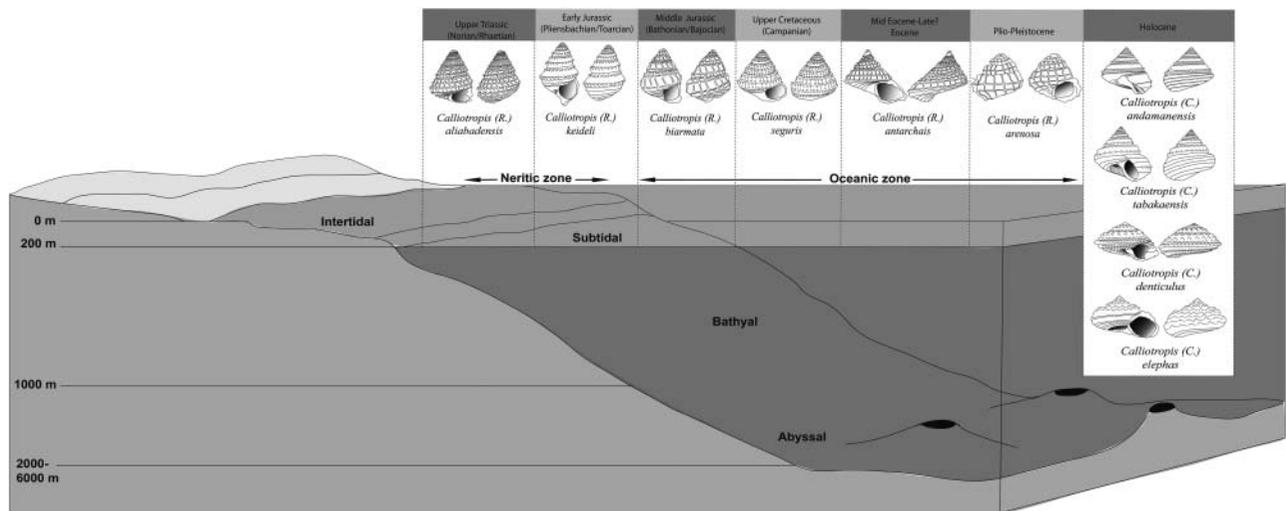
Figure 9. Hypothetical evolutionary onshore–offshore pattern in *Calliotropis* shell phenotypes through the geological record and following a bathymetric gradient. Note that the highest diversity of *Calliotropis* shell morphologies occurs in the Holocene.

history strategies and genetic population structures. Thus, abiotic gradients may also be thought to have imposed differences in speciation and extinction rates, and taxonomic durations within calliotropid benthic communities. Hickman (2016) argued that the elevated deep-water diversity of the Holocene calliotropid gastropods from the Indo-Pacific region and Indonesia cannot be understood without geological and regional tectonic history, related to the openings and closings of distinct deep-water basins, gulfs and straits and to the movements and accretion of microplates. This most probably gave rise to several ecological microhabitats in which the Holocene calliotropid fauna could have evolved towards a high diversity. A clear example is *C. (C.) pelseneeri*, a living Antarctic species which seems to have expanded into higher latitudes as well as deep water habitats during the Holocene. *Calliotropis (C.) pelseneeri* shows a particular shell pattern and ornamentation (see above) very different than other typical living calliotropids; this may support the idea of a high morphological diversity of the genus in Cenozoic times related to latitudinal migrations and geological tectonic history.

Levinton (1988) pointed out that the greater habitat extinction rate onshore could have permitted evolutionary experimentation, whereas biotas in more offshore environments may have been too densely packed and too persistent to permit much evolutionary divergence.

Conclusions

The excellent preservation of calliotropid shells from the Middle Jurassic of Poland allows detailed description of the morphological characters of the embryonic shell in some Mesozoic representatives of *Calliotropis*, emendation of the diagnosis of the characteristic Jurassic species of this genus, *Calliotropis (Riselloidea) biarmata* (Münster, 1844), and description of two new species – *Calliotropis (Riselloidea) faustiankensis* sp. nov. and *Calliotropis (Riselloidea) lukovensis* sp. nov. – from the Bathonian and Callovian of Faustianka and Łuków, respectively.

Cluster and principal component analyses based on shell characters selected from extinct and modern species of *Calliotropis* produced two easily discernible morphological groups which we interpret as corresponding to the two subgenera of *Calliotropis* proposed by Ferrari *et al.* (2014): *Calliotropis (Riselloidea)* includes majority of the Mesozoic species, and *Calliotropis (Calliotropis)* contains the majority of the Recent species. Nevertheless, some taxa deviate from this pattern, i.e. Recent *Calliotropis (C.) pelseneeri*, *C. (C.) chalkeie*, *C. (C.) conoeides* and *C. (C.) enantioserrata*, and Jurassic *Calliotropis (R.) erratica* and *C. (R.) keideli*]. The revised diagnosis of the subgenus *Calliotropis (Riselloidea)* groups shallow-reef ecophenotypes that have strong and reticulate ornament patterns consisting of two or three primary spiral cords, additional secondary spiral cords visible towards mature growth stages which are intercepted by axial ribs forming conspicuous nodes at the crossing points and spinose nodes at the periphery of whorls, lack a widely opened umbilicus, have high- to moderately high-spired and medium-sized shells, and a more depressed protoconch than those of living forms ornamented by several pits forming a net-like pattern. In contrast, the subgenus *Calliotropis (Calliotropis)* groups deep-water ecophenotypes with a simpler and less reticulate ornamentation, where the third or fourth strong spiral cord is infrequent on mature whorls and nodes are generally smaller and less conspicuous than those of the fossil species; they also generally show a widely open and funnel-shaped umbilicus, have a nearly flat top, range from very small to very large in size, usually have a columellar denticle, a reflected outer lip and a descending aperture, while the protoconch is generally more bulbous than those of fossil forms, and smooth or glassy. The morphological differences between extinct and extant representatives of *Calliotropis* may be interpreted preliminarily as a response to different environments, with migration from shallow marine settings during most of Mesozoic times towards bathyal depths in the Cenozoic to Recent.

Acknowledgements

References

Bandel, K. 2010. Relationships of the Triassic Eucycloidea Koken, 1897 (Mollusca, Gastropoda) to modern genera such as *Pagodatrochus*, *Calliotropis* and *Euchelus*, based on morphology of the early shell. *Bulletin of Geosciences*, **85**, 435–486.

Böckh, J. 1874. A Bakony déli részének földtani viszonyai. IL rész. (Die geologischen Verhältnisse des südlichen Theiles des Bakony. IL). *Annales Institut Geológia Publia Hungária*, **3**, 1–18.

Bouchet, P., **Rocroi, J.-P.**, **Hausdorf. B.**, **Kaim, A.**, **Kano. Y.**, **Nützel, A.**, **Parkhaev, P.**, **Schrödl, M.** & **Strong E.** 2017. Revised classification, nomenclator and typification of gastropod and monoplacophoran families. *Malaocologia*, **61**(1–2), 1–495.

Brösamlen, R. 1909. Beitrag zur Kenntnis der Gastropoden des schwäbischen Jura. *Palaeontographica*, **56**, 177–321.

Brusina S. 1865. Conchiglie dalmate inedite. *Verhandlungen der Zoologisch-Botanischen Gesellschaft in Wien*, **15**, 3–42.

Calzada, S. 1989. Algunos troquidos neocretacicos del Prepirineo catalan. *Batalleria*, **3**, 23–36.

Conti, M. A. A. & **Monari, S.** 2001. Middle Jurassic gastropods from the Central High Atlas; Morocco. *Geobios*, 34, 183–214.

Cossmann, M. 1888. Note rectificative sur la nomenclature d'un genre de coquilles fossiles. *Journal de Conchyliologie*, **36**, 1–335.

Cossmann, M. 1895. *Essais de paléoconchologie comparée 1.* Privately published, Paris, 159 pp.

Cossmann, M. 1909. *Essais de paléoconchologie comparée.* Privately published, Paris, 248 pp.

Cossmann, M. 1924. Extension dans les Deux−Sèvres de la faune du Callovien de Montreuil−Bellay. *Mémoires Société Géologique et Minéralogique de Bretagne*, **1**, 1–53.

Cox, L. R. 1960. Family Nododelphinulidae Cox, n. fam. P. 308 in R. C. Moore & W. Pitrat (eds) *Treatise on invertebrate paleontology. Mollusca 1, Part I.* Geological Society of America and University of Kansas Press, Boulder and Lawrence.

Cuvier, G. 1795. Second mémoire sur l'organisation et les rapport des animauxà sang blanc, dans lequl on traite de la structure des Mollusques et de leur division en orders, luà la Société d'histoire naturelle de Paris, le 11 Prairial, an III. *Magazin Encyclopédique, ou Journal des Sciences, des Letters et des Arts*, **2**, 433–449.

Darragh, T. A. 1997. Gastropoda, Scaphopoda, Cephalopoda and new Bivalvia of the Paleocene Pebble Point Formation, Victoria, Australia. *Proceedings of the Royal Society of Victoria*, **109**, 57–108.

Das, S. Bardhan, S. & **Lahiri, T.** 1999. The Late Bathonian gastropod fauna of Kutch, western India – a new assemblage. *Paleontological Research*, **3**, 268–286.

Ferrari, S. M., **Kaim, A.** & **Damborenea S.** 2014. The genera *Calliotropis* Seguenza and *Ambercyclus* n. gen. (Vetigastropoda, Eucyclidae) from the Early Jurassic of Argentina. *Journal of Paleontology*, **88**, 1174–1188.

Gedl, P. & **Kaim, A.** 2012. An introduction to the palaeoenvironmental reconstruction of the Bathonian (Middle Jurassic) ore-bearing clays at Gnaszyn, Kraków-Silesia Homocline, Poland. *Acta Geologica Polonica*, **62**, 267–280.

Geiger, D., **Nützel, A.** & **Sasaki, T.** 2008. Vetigastropoda. Pp. 297–330 in W. Ponder, & D. L. Lindberg, (eds) *Phylogeny and evolution of the Mollusca.* University of California Press, Berkeley.

Greppin, E. 1898. Description des fossiles de la Grande Oolithe des environs de Bâle. *Mémoires de la Société paléontologique Suisse*, **15**, 1–137.

Gründel, J. 1975. Gastropoden aus dem Dogger. III. Rissoinidae, Eucyclidae und Trochidae. *Zeitschrift für Geologische Wissenschaften*, **3**, 239–251.

Gründel, J. 1990. Gastropoden aus Callov−Geschieben aus dem Nordosten Deutschlands. II. Mathildidae, Trochacea, Palaeotrochacea, Amberleyacea, Rissoinidae, Pleurotomariidae und Purpurinidae. *Zeitschrift für Geologische Wissenschaften*, **18**, 1137–1151.

Gründel, J. 2000. Archaeogastropoda aus dem Dogger Norddeutschlands und des nordwestlichen Polens. *Berliner Geowissenschaftliche Abhandlungen Reihe E*, **34**, 205–253.

Gründel, J. 2003a. Gastropoden aus dem Bajocian und Bathonium von Sengenhtal und Kinding, Franken (Süddeutschland). *Zitteliana*, **A43**, 45–91.

Gründel, J. 2003b. Die Gastropoden der Dogger-Geschiebe Deutschlands und des nordweslichen Polens. *Archiv für Geschiebekunde*, **4**(3–4), 129–240.

Gründel, J. & **Koppka, J.** 2007. Gastropoden aus einem Lias-Geschiebe von Lentschow bei Lassan (Vorpommern, Nordostdeutschland). *Archiv für Geschiebekunde*, **4**(10), 643–658.

Gründel, J., **Bosch, K.**, **Dietze, V.**, **Franz, M.** & **Kutz, M.** 2012. Die Gastropoden aus dem Mittleren Jura vom Kahlenberg bei Ringsheim/Baden-Wurttemberg (Suddeutschland). *Beringeria*, **42**, 5–44.

Habe, T. & **Ando, Y.** 1980. New minute gastropod, *Pandorbis japonica* from Japan (Cyclostrematidae). *Japanese Journal of Malacology*, **38**(4), 227–228.

Hammer, Ø., **Harper, D. A. T.** & **Ryan, P. D.** 2001. PAST: Paleontological statistics software package for education and data analysis. *Palaeontologia Electronica*, **4**, 1–9.

Hébert, E. & **Eudes−Deslongchamps, E.** 1860. Mémoire sur les fossiles de Montreuil−Bellay (Maine−et−Loire). 1re. partie. Céphalopodes et Gastéropodes. *Bulletin de la Société Linnéenne de Normandie*, **5**, 153–240.

Helwerda, R. A., **Wesselingh, F. P.** & **Williams, S. T.** 2014. On some Vetigastropoda (Mollusca, Gastropoda) from the Plio-Pleistocene of the Philippines with descriptions of three new species. *Zootaxa*, **3755**, 101–135.

Hickman, C. 2016. New species of deep-sea gastropods from the Indo-West Pacific region (Gastropoda: Vetigastropoda: Seguenzioidea: Calliotropidae) with a geologic and biogeographic perspective. *The Nautilus*, **130**(3), 83–100.

Hickman, C. S. & **McLean, J. H.** 1990. Systematic revision and suprageneric classification of trochacean gastropods. *Science Series, Natural History Museum of Los Angeles County*, **35**, 1–169.

Jablonski, D. & **Bottjer, D. J.** 1990. Onshore-offshore trends in marine invertebrate evolution. Pp. 21–75 in R. M. Ross & W. D. Allmon (eds) *Causes of evolution: A paleontological perspective.* University of Chicago Press, Chicago.

Jaitly. A. K., **Szabó, J.** & **Fürsich, T.** 2000. Contributions to the Jurassic of Kachchh, western India. VII. The gastropod fauna. Part I. Pleurotomarioidea, Fissureloidea, Trochoidea and Eucycloidea. *Beringeria*, **27**, 31–61.

Jeffreys, J. G. 1876. Preliminary report of the biological results of a cruise in H.M.S. *Valorous* to Davis Strait in 1875. *Proceedings of the Royal Society*, **25**, 177–230.

Kaim, A. 2004. The evolution of conch ontogeny in Mesozoic open sea gastropods. *Palaeontologia Polonica*, **62**, 3–183.

Kaim, A. 2008. A review of gastropods from a Callovian (Middle Jurassic) glacial drift at Łuków, Eastern Poland. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 247, 161–176.

Kano, Y. 2008. Vetigastropod phylogeny and a new concept of Seguenzioidea: independent evolution of copulatory organs in the deep-sea habitats. *Zoologica Scripta*, **37**, 1–21.

Kano, Y., **Chikyu E.** & **Warén A.** 2009. Morphological, ecological and molecular characterization of the enigmatic planispiral snail genus *Adeuomphalus* (Vetigastropoda: Seguenzioidea). *Journal of Molluscan Studies*, **75**, 397–418.

Kiel, S. & **Bandel, K.** 2001. Trochidae (Archaeogastropoda) from the Campanian of Torallola in northern Spain. *Acta Geologica Polonica*, **5**(2), 137–154.

Koken, E. 1897. Die Gastropoden der Trias um Hallstadt. *Abhandlungen der K. K. Geologischen Reichsanstalt*, **17**(4), 1–112.

Levinton, J. 1988. *Genetics, paleontology, and macroevolution.* Cambridge University Press, New York, 637 pp.

Linsley, R. M. 1977. Some laws of gastropod shell form. *Paleobiology*, **3**, 196–206.

Linsley, R. M. 1978. Locomotion rates and shell form in the Gastropoda. *Malacologia*, **17**, 193–206.

Marshall, B. A. 1979. The Trochidae and Turbinidae of the Kermadec Ridge (Mollusca: Gastropoda). *New Zealand Journal of Zoology*, **6**, 521–552.

Marshall, B. A. 1983. Recent and Tertiary Seguenziidae (Mollusca: Gastropoda) from the New Zealand region. *New Zealand Journal of Zoology*, **10**, 235–261.

Marshall, B. A. 1991. Mollusca Gastropoda: Seguenziidae from New Caledonia and the Loyalty Islands. *Mémoires du Muséum National d'Histoire Naturelle, Série A*, **150**, 41–109

Matyja, B. A. & **Wierzbowski, A.** 2000. Ammonites and stratigraphy of the uppermost Bajocian and Lower Bathonian between Częstochowa and Wieluń, Central Poland. *Acta Geologica Polonica*, **50**, 191–209.

Münster, G. G., **zu.** 1844. Molluscorum Gasteropodum Reliquiae. Pp. 1–128 in G. A. Goldfuss (ed.) *Petrefacta Germaniae. Dritter Theil*. Arnz, Düsseldorf, 128.

Nützel, A. & **Senowbary-Daryan, B.** 1999. Gastropods from the Late Triassic (Norian–Rhaetian) Nayband Formation of Central Iran. *Beringeria*, **23**, 93–132.

Nützel, A., **Hamedani, A.**, **Senowbari-Daryan, E.** & **Senowbari-Daryan, B.** 2003. Some Late Triassic gastropods from the Nayband Formation in Central Iran. *Facies*, **48**, 127–134.

Philippi, R. A. 1844. *Enumeratio Molluscorum Siciliae. Volumen Secundum*. E. Anton, Halis Saxonum, 303 pp.

Philippi, R. A. 1846–1855. Die Kreiselschnecken oder Trochoideen, *Trochus*. Pp. 1–372 in F. H. W. Martini & J. H. Chemnitz (eds) *Systematisches Conchylien–Cabinet. Band 2, Abtheilung 3*. Bauer & Raspe Nürnberg.

Ponder, W. F. & **Lindberg, D. R.** 1997. Towards a phylogeny of gastropod molluscs: an analysis using morphological characters. *Zoological Journal of the Linnean Society*, **119**, 83–265.

Powell, A. W. B. 1958. Mollusca of the Kermadec Islands. *Records of the Auckland Institute & Museum*, **5**, 65–85.

Salvini-Plawen, L. V. 1980. A reconsideration of systematics in the Mollusca (phylogeny and higher classification). *Malacologia*, **19**, 249–278.

Sasaki, T. 1998. Comparative anatomy and phylogeny of the Recent Archaeogastropoda (Mollusca: Gastropoda). *The University of Tokyo Bulletin*, **38**, 1–223.

Seguenza, G. 1876. Studii stratigrafici sulla formazione pliocenica dell'Italia Meridionale. *Bollettino del reale Comitato Geologico d'Italia*, **7**, 7–15.

Seguenza, G. 1902. Molluschi poco noti dei Terreni Terziarii di Messina. Trochidae e Solariidae. *Bollettino della Società Geologica Italiana*, **21**, 455–465.

Sohl, N. F. 1964. Gastropods from the Coffee Sand (Upper Cretaceous) of Mississippi. *United States Geological Survey Professional Paper*, 331–C, 345–394.

Stilwell, J. 2005. A new species of *Calliotropis* (Mollusca: Gastropoda: Vetigastopoda: Trochidae: Eucyclinae) from the Eocene of Antarctica. *Molluscan Research*, **25**, 9–13.

Szabó, J. 1982. Lower and Middle Jurassic Gastropods from the Bakony Mountains (Hungary). Part IV: Neritacea, Craspedostomacea, Amberleyacea (Archaeogastropoda). *Annales Historico-Naturales Musei Nationalis Hungarici*, **74**, 17–33.

Szabó, J. 1995. Eucyclidae (Eucycloidea), Gastropoda) as a Liassic palaeontological index in the Transdanubian Central Range (Hungary). *Hantkeniana*, **1**, 67–74.

Szabó, J. 2009. Gastropods of the Early Jurassic Hierlatz Limestone Formation; Part 1: a revision of type collections from Austria and Hungarian localities. *Fragmenta Palaeontologica Hungarica*, **26**, 1–108.

Vermeij, G. J. 1977. The Mesozoic Marine Revolution: evidence from snails, predators and grazers. *Paleobiology*, **3**, 245–258.

Vermeij, G. J. 1987. *Evolution and escalation*. Princeton University Press, Princeton, 527 pp.

Vermeij, G. J. 1993. *A natural history of shells*. Princeton University Press, Princeton, 207 pp.

Verrill, A. 1884. Second catalogue of Mollusca recently added to the fauna of the New England coast and the adjacent part of the Atlantic, consisting mostly of deep-sea species, with notes on others previously recorded. *Transactions of the Connecticut Academy of Arts and Sciences*, 6(1), 139–144.

Vilvens, C. 2004. Description of four new species of *Calliotropis* (Gastropoda: Trochidae: Eucyclinae: Calliotropini) from New Caledonia, Fiji and Vanuatu. *Novapex*, **5**, 19–31.

Vilvens, C. 2007. New species and new records of *Calliotropis* (Gastropoda: Chilodontidae: Calliotropinae) from Indo-Pacific. *Novapex*, **8** (HS 5), 1–72.

Vilvens, C. & **Sellanes, J.** 2010. Description of *Calliotropis caciliae* new species (Gastropoda: Chilodontidae: Aclliotropinae) from Chile. *The Nautilus*, **124**, 107–111.

Wagner, P. & **Erwin, H.** 2006. Patterns of convergence in general shell form among Paleozoic gastropods. *Paleobiology*, **32**, 316–337.

Watson, R. B. 1879. Mollusca of HMS Challenger Expedition. IV. Trochidae continued, viz. the genera *Basillisa* and *Trochus*, and the Turbinidae, viz. the genus Turbo. *Journal of the Linnean Society, Zoology*, **14**, 692–716.

Wenz, W. 1938. Gastropoda. Teil 2: Prosobranchia. Pp. 241–480 in O. H. Schindewolf (ed.) *Handbuch der Paléozoologie, Band 6*, Gebrüder Borntraeger, Berlin.